STUDIES OF BIOLOGY AND BEHAVIOR OF THE DOUGLAS-FIR
TUSSOCK MOTH-1966

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Progress Report

STUDIES OF BIOLOGY AND BEHAVIOR OF THE
DOUGLAS-FIR TUSSOCK MOTH - 1966

By

Richard R. Mason, Research Entomologist
Jerrold W. Baxter, Biological Aid

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SUMMARY

Studies were initiated in the summer of 1966 on biology and behavior of the Douglas-fir tussock moth in a declining outbreak in northern California. An unusually late spring frost killed most of the new tip growth on white fir branches and deprived young tussock moth larvae of their preferred food. This situation prompted a number of short experiments on food quality not originally anticipated. Other studies were carried out on larval behavior in a natural forest environment.

Major findings of these studies were as follows:

1. All larval instars fed more on new foliage than on old. Old needles were almost totally unacceptable to early instar larvae, but were fed on by late instars. When new fir foliage was not available in the field larvae often migrated to pine where they fed on new needles. However, in the laboratory new fir foliage, when available, was favored over new pine foliage.

2. Lack of acceptable food for early instar larvae stimulated wandering in the laboratory. In the field this probably results in considerable larval dispersal. When larvae were fed only frost-damaged foliage which contained no new growth a large number died, apparently of starvation. Survivors on damaged foliage were stunted and developed slower than larvae that were fed normal foliage.

3. Female moths reared in the laboratory contained an average of 200 eggs per individual, but this was considerably higher than the average number of eggs per mass in the field. Fecundity is directly related to body size and can probably be estimated accurately from measurements of the moth.

4. Larvae tend to avoid high light intensities and temperatures by remaining on the underside of branches and needles that are exposed to the sun. Most activity and feeding by late instar larvae occurred in the evening, night and early morning; these were especially avoided at mid-day.

5. Early instar larvae usually concentrated in the vicinity of new buds; later instars fed further back on the branch as the season progressed. Larvae almost always remained in foliated portions of the tree.

6. Recommendations for further research on tussock moth biology are listed.

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and
Jerrold W. Baxter, Biological Aid

INTRODUCTION

Few aspects of the biology of the Douglas-fir tussock moth have been
studied in depth. General observations on habits have been reported
by various authors, but precise information, especially on field
behavior, is lacking (Balch, 1932; Dodge and Trostle, 1964; Keen,
1952). Edwards (1965) investigated activity rhythms of the tussock
moth in the laboratory which represents the best information avail-
able on its behavior. These studies, however, were not concerned
with direction of insect movement as it would occur in a tree under
natural field environment. Moreover, the orientation of larvae to
natural stimuli, particularly as these might affect the position
that larvae take in the tree, was not studied in detail. In general,
there is a dearth of knowledge on this phase of tussock moth biology,
particularly under natural conditions.

Information on behavioral patterns is vital to several aspects of the
current tussock moth research effort at the Pacific Northwest Forest
and Range Experiment Station. This fact has been spelled out in Item
4B of a joint prospectus on research needs prepared by the Station
and Region Six of the Forest Service. [1]

Methods of population assessment usually assume that larvae are
reasonably well distributed on the branch foliage being sampled.
Unusual migrations to the inner portions of the branch or to the
main bole would result in gross errors of estimation. Similarly,
migratory patterns and intermingling of larvae may have a signifi-
cant influence on initiation and spread of a disease-causing virus
which is an important factor in the termination of most tussock moth

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[1] Prospectus for a Joint Research-Administrative Effort to Develop
and Test a Method for Using a Nuclear-Polyhedrosis Virus Against the
Douglas-fir Tussock Moth. U. S. Forest Service, Portland, Oregon.
March 23, 1966.

outbreaks. Feeding habits involving selection, preference and rhythms
are also important, particularly since the virus is presumably trans-
mitted to the insect on its food. It is obvious that much information
is needed on tussock moth biology and behavior, especially under field
conditions. Such information would be an important contribution to the
present research program.

The information in this report is the result of field and laboratory
studies carried out in a Douglas-fir tussock moth outbreak during the
summer of 1966. The outbreak was located in the Corral Creek area,
within the general boundaries of the Modoc National Forest in northern
California. The forest type in this area is predominantly an overstory
of old growth ponderosa pine, *Pinus ponderosa* Laws, mixed with a moderate
to heavy understory of white fir, *Abies concolor* (Gord. and Glend.).

Due to rapid development of larvae and an early collapse of the popu-
lation many of the behavioral studies were short and limited in scope.
Field research on insects frequently must be opportunistic in order to
profit from sudden developments which cannot always be foreseen in
advance. Such was the case with some of these studies which were
established and carried out quickly to take advantage of rapidly changing
situations and limited facilities and manpower. The results, however,
have the added value in most instances of being truly realistic of
events that take place in a natural forest.

OBJECTIVES

Principal aims of these studies were to fill in gaps where knowledge
of tussock moth biology is lacking. Emphasis was placed on studies of
behavioral patterns which might influence population sampling methods
that were being developed concurrently at the same location. Because
of an unusually late frost which killed much of the new needle growth
on white fir some shift in plans was necessary so that the effect of
this phenomenon on tussock moth larvae could be investigated. General
objectives for the summer's studies were as follows:

1. To determine the effect of the late frost on larval development and
behavior.

2. To determine lateral and vertical distribution of larvae in the
host tree.

3. To observe the influence of external stimuli, particularly tempera-
ture and light, on orientation and movement of larvae.

4. To observe larval dispersal and migration patterns.

5. To collect general information on tussock moth life history and
biology.

THE STUDIES

Influences of Late Frost and Food Quality

Newly hatched larvae of the tussock moth feed almost entirely on new
foliage (Dodge and Trostle, 1964). Eclosion, in fact, seems to be
synchronized with bud burst in the spring so that young foliage is
available for the first instar larvae. Due to an unseasonably warm
spring, flushing of white fir needles was underway on May 16 when
the study site at Corral Creek was first visited for the season.
Maximum temperatures in the latter half of May frequently reached
into the mid 80's each day. No hatching was yet observed at that
time, but there is reason to believe that it had probably commenced
at some locations. The first larvae were observed on May 25 and
some of these were well into the first instar. By this time, the
most advanced needle growth in upper crowns was about an inch in
length. After leaving the egg mass larvae clustered on the ends
of twigs and fed along the mid-rib on the underside of new needles.

On June 1 and 2 temperatures dropped to 34° F and about two inches
of snow fell in the outbreak area. Larvae became immobile on the
needles or, if they were only newly hatched, did not migrate from
the mass. In the early morning of June 3 the thermograph at the
site recorded a minimum of 27° F, followed by 30° the next morning.
These temperatures froze almost all advanced new growth on white
fir over much of the study area (Figure 1). Killing of new growth
at the branch tips was so severe that most trees produced no secondary
growth flushes. Current needle complement was completed only where
buds were undamaged, either on whole trees that were late in initiating
growth or on parts of trees in the lower crown where flushing was
slower than in the rest of the crown.

The destruction of virtually all new needle growth on fir would suggest
a catastrophic effect on early instar larvae, which feed almost ex-
clusively on new foliage. Young larvae on damaged trees would either
have to locate suitable food elsewhere or resort to fir needles at
least a year old. In either case, larvae would be subjected to an
abnormal stress that might well influence behavior or development
and have an ultimate effect on population trend. The unexpected damage
from frost, therefore, created a rather unique opportunity to study
the effects of food quality on a natural population.

1. Field studies of larval feeding

Some trees were not seriously damaged by the frost, especially those in
localities where microclimates were such that many trees had not yet
initiated growth. In such locations, three pairs of trees were selected

so that one tree in each pair had all new foliage killed, and the adjacent tree had undamaged foliage. A sleeve cage, 18 inches long and 6 inches in diameter covered with nylon screen, was then placed over a representative branch on each of the six trees (Figure 2). Each pair of cages was installed similarly in respect to all conditions except the difference of foliage within. Twenty larvae, mostly in the third instar, were collected at random from the field and placed in each cage. Comparative feeding was estimated by periodically measuring the volume of frass produced in each cage.

All larvae in one cage died (presumably of virus disease) before any measurements could be made. Also, differential mortality in the other cages prevented an analysis by pairs, by obscuring differences due to foliage from differences due to unequal numbers of larvae. However, over the period of study similar numbers of live larvae fed on the two types of foliage at any given time, although there was a progressive loss of larvae from mortality on both foliage types. Using cumulative frass production as an index of feeding, results were summarized for each of the two types of foliage (Figure 3). Considerably more feeding occurred in cages with new foliage than in those with damaged foliage, especially among early instar larvae. The similar slope of trend lines later in the summer indicates that late instar larvae may have accepted and fed as well on old needles as on new foliage.

2. Laboratory studies

Other possible effects of foliage condition on larval behavior were investigated further in the field laboratory (Figure 4). Ten rearing trays 4" x 14" x 18" were constructed with muslin bottoms, and tree tanglefoot was placed around the upper edge to confine the larvae. Half the trays were provided with a 15-inch twig with new undamaged foliage; the other half were provided with twigs of the same size but with all current growth killed by frost. A water vial with cotton plug was attached to each stem to inhibit drying of the foliage. Trays were placed side by side in the laboratory and each provided with 25 second-or third-instar larvae collected at random from the field. As foliage was depleted or dried out, twigs were replaced in the trays with fresh material. Trays were examined at regular intervals thereafter for number of surviving insects, their location in the tray and their stage of development. Results are described in the following sections.

    a. Larval movement. Location of larvae in each tray depicted in a general way the acceptance of the two types of foliage as food. If foliage was suitable, larvae spent most of their time among the needles at the feeding site; if available foliage was not acceptable, the larvae fed little and wandered

Figure 1. New growth on white fir damaged by late spring frost.

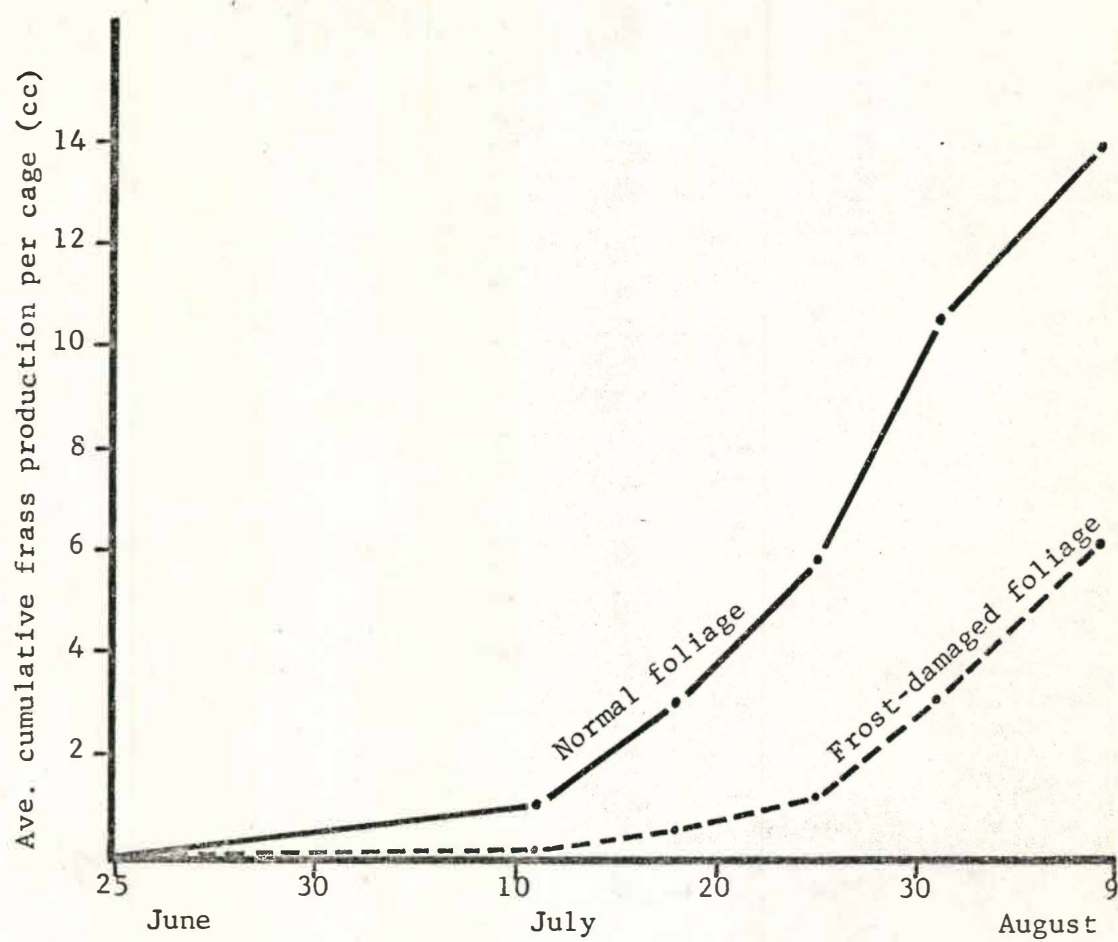Figure 2. Sleeve cages on branches of white fir.

Figure 3. Frass production by larvae feeding on normal and frost-damaged foliage in field cages.

about the tray. Therefore, the position of larvae in the
tray when examined reflected degree of movement which was
largely determined by food palatability. Other factors
such as molting, disease, parasitism, and preparation for
pupation also influenced movement somewhat, but probably
to a minor degree until the later instars.

Figure 4. Laboratory trailer at temporary location at Corral
Creek infestation.

Results are illustrated in Figure 5. On June 27 and July 1
several times as many larvae were wandering about in the trays
with frost-damaged foliage as in trays with normal foliage.
Differences in the amount of wandering in the two types of
foliage trays on these dates are highly significant (p=.01).
Thereafter, survival in trays with damaged foliage dropped
sharply so that comparisons in July are not strictly valid;
nevertheless, the data indicate a trend. Third- and fourth-
instar larvae on damaged foliage wandered a great deal more
than the same age larvae on normal foliage; later instars
seemed to wander approximately the same in the presence of new
growth as in old. This evidence is corroborated somewhat by
the field feeding studies (Figure 3) where frass production on
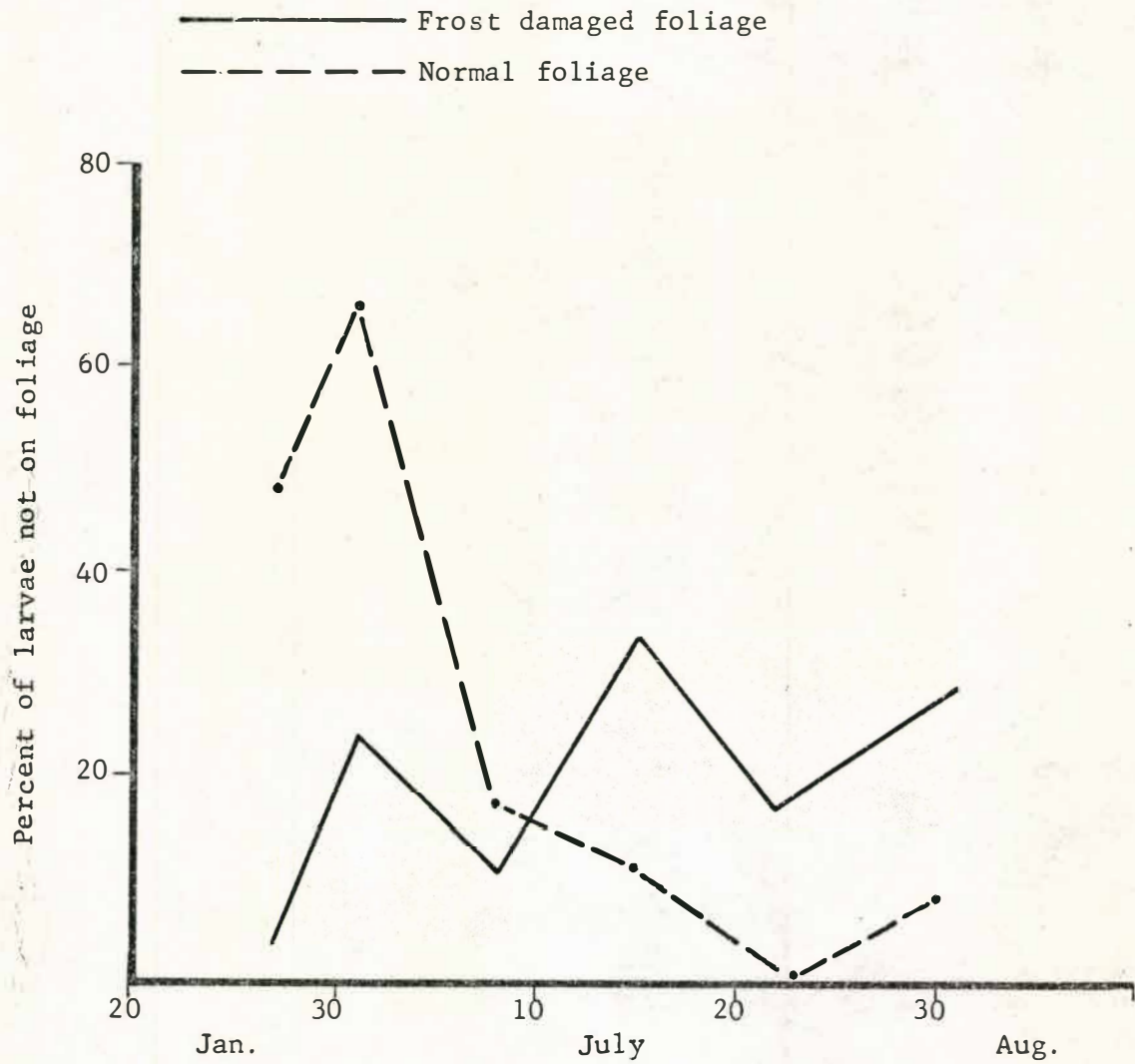damaged foliage rose markedly after the fourth instar, indicating

Figure 5.   Location of larvae in rearing trays in the laboratory when offered frost-damaged foliage and normal foliage from white fir.

that old foliage was more suitable for late instar larvae than early instars. Presumably, movement off of damaged foliage by the first and second instars would have been particularly pronounced had it been studied, since old foliage seems to be almost totally unacceptable in these stages.

In natural situations where desired food is scarce, wandering would have important survival value to larvae because it increases their chances of coming into contact with edible foliage. Food scarcity in the study area undoubtedly stimulated intense movement among the early instars and resulted in dispersal, both by crawling and traveling through the air on silk threads.

b. Survival. Larvae reared in trays began to suffer signifi-
cant mortality about a week after collection from the field.
An attempt was made to assign a cause of death to all dead larvae. Diagnostic symptoms of parasitism and virus disease were relatively easy to recognize, but frequently the cause of death was unknown. Once larvae were removed from the field they were no longer subject to parasitism and were probably abnormally affected by disease so that death in the cohort from these two factors was unnatural.

During the first week in the laboratory no larvae died, but thereafter a significant number succumbed, especially among those reared on damaged foliage (Figure 6, Part A). After a month, when pupation began in trays with normal foliage, 52 percent of the larvae on new growth had survived while only 12 percent of the original 125 on frost-damaged twigs remained. Part B of Figure 6 shows that major losses among larvae on damaged foliage were due to causes other than disease or parasites and, thus, are listed as unknown. Based on what is now known about food quality and acceptance by early instar larvae it would seem logical that the bulk of unknown mortality was actually due to starvation. The highest death rates among larvae on old foliage occurred in the third and fourth instars, and mortality during this period ultimately accounted for at least 74 percent of the total cohort in that group of trays. Furthermore, general observation indicated that death occurred most frequently among larvae that had not accepted food in the trays and were wandering about. This evidence seems to confirm that lack of suitable food can cause significant starvation among early instar larvae of the tussock moth. In the field, however, the influence of a late frost and its effect on young larvae, through
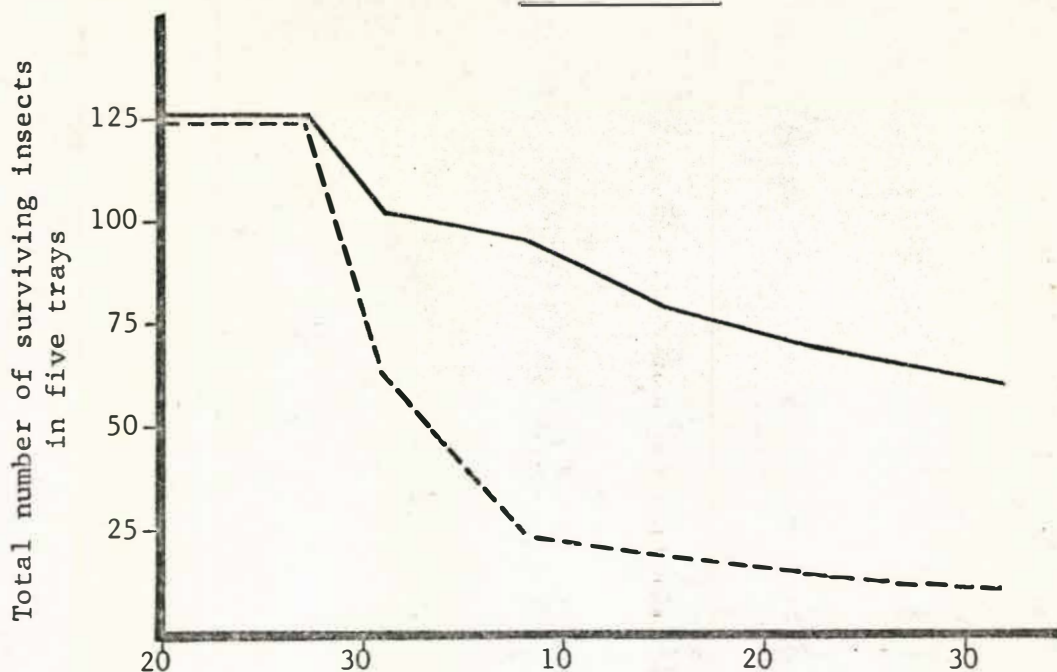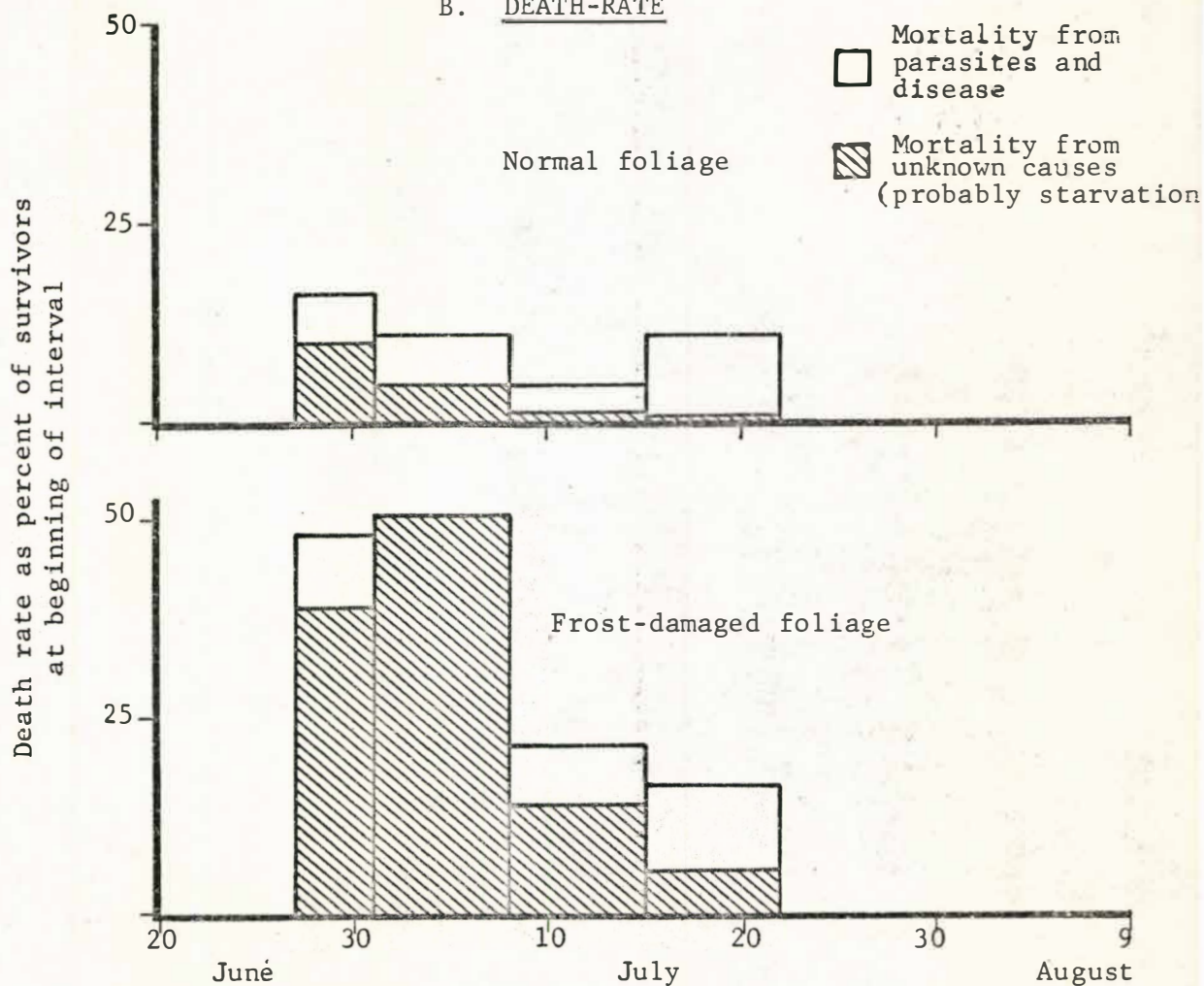
Figure 6. Survival and death-rate of Douglas-fir tussock moth larvae
reared in laboratory on two kinds of white fir foliage.

reducing the food supply, is probably tempered somewhat by the ability of early instars to disperse effectively and eventually locate palatable foliage.

Ultimately, 36 adult moths (15 females and 21 males) emerged from trays with normal foliage while only 5 adults (1 female and 4 males) completed development in trays with damaged foliage. Survival of each cohort of 125 larvae was, thus, 29 percent on current needles and 4 percent on old needles.

c. Development. Larvae reared on damaged foliage also developed at a somewhat slower rate than those that fed on normal foliage. At the time of collection from the field both groups were identical, but by mid-July stage structure of survivors in each group was different. Pupation occurred first and adults emerged almost two weeks earlier from trays with normal foliage than from trays with frost-damaged foliage (Figure 7). Moreover, survivors on old growth foliage appeared to be somewhat smaller although no measurements were made. Since late instar larvae fed almost equally as well on old needles as on new growth, differences in development rate at that stage were apparently due to earlier nutritional deficiencies. This emphasizes the influence that food quality has, not only on survival of current feeding insects, but on their subsequent life stages.

d. Fecundity. Thirteen female adults that emerged from trays were examined further for egg potential, especially in relation to their size. After being preserved for several weeks in 70 percent alcohol the volume of each adult was measured by submerging the moth in a graduated cylinder and reading the displacement. Then the abdomens were dissected and all eggs counted with the aid of a binocular microscope.

The relationship between size of female and number of eggs is shown in Figure 8. A curvilinear relationship would probably be more appropriate and fit the data better than the straight line that was computed. Size of individual moths varies considerably and is directly proportional to fecundity. This suggests that factors which might influence insect size, such as food or larval density, may also affect fecundity. Paradoxically, the only female moth that emerged from trays with damaged foliage contained the largest number of eggs (272). The average fecundity of laboratory reared moths was somewhat higher (200 eggs) than the average number of eggs in masses (161) that were sampled from the field in the Spring.

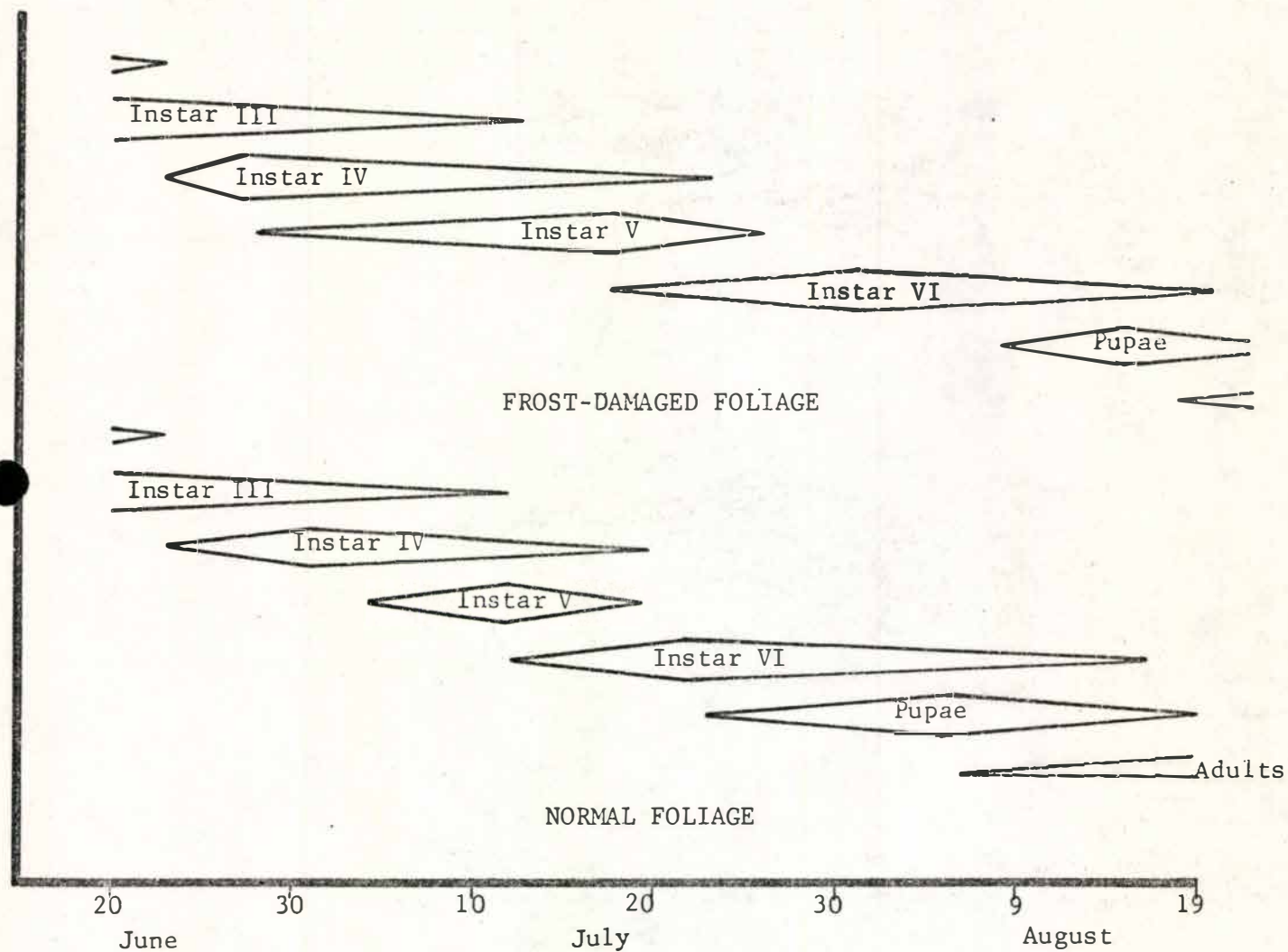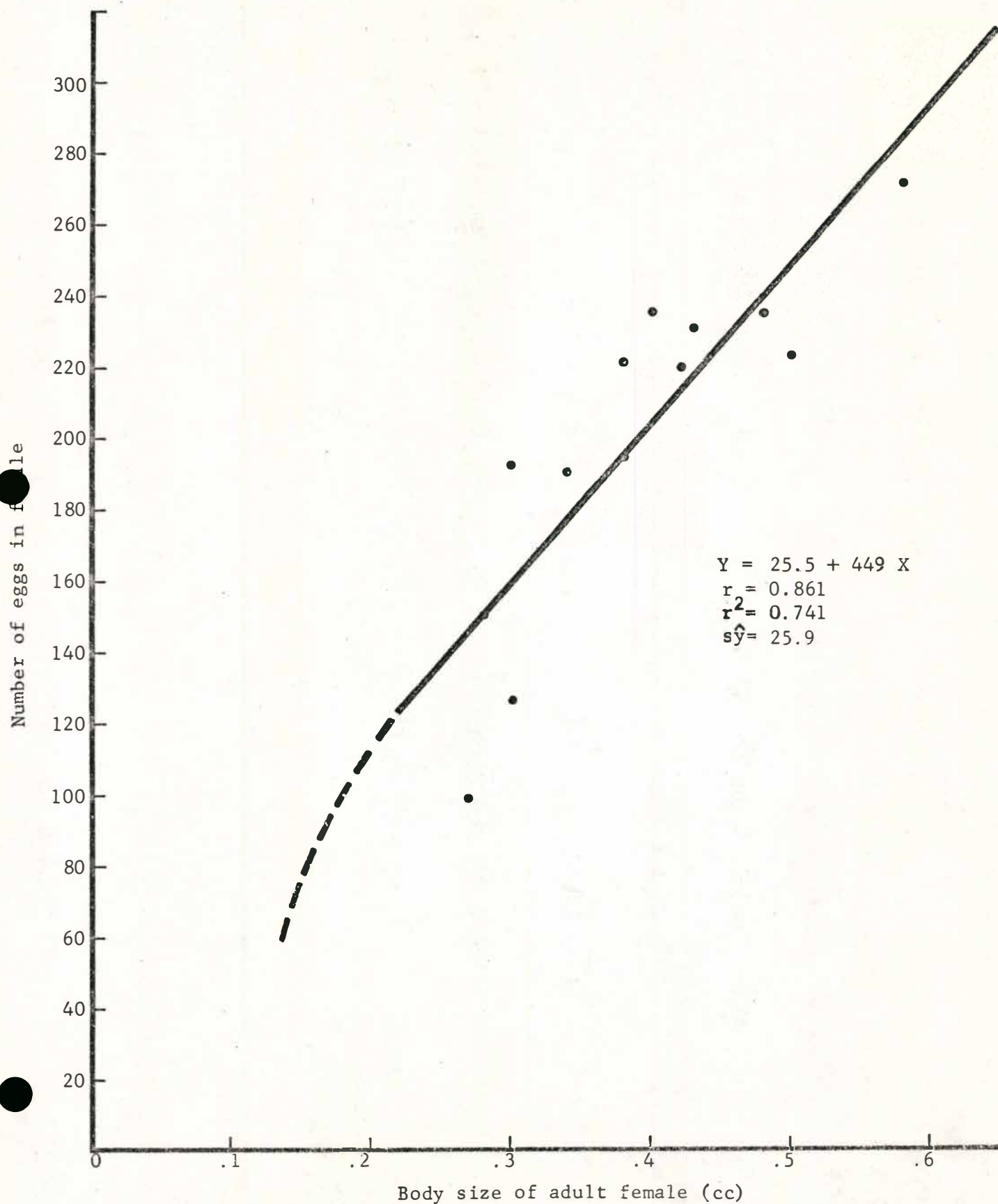e. Host selection. In late June, third- and fourth-instar larvae were frequently observed feeding in the understory on new growth

Figure 7. Development of the Douglas-fir tussock moth in a field laboratory
on frost-damaged foliage and normal foliage of white fir.

$$Y = 25.5 + 449 X$$
$$r = 0.861$$
$$r^2 = 0.741$$
$$s\hat{y} = 25.9$$

Figure 8. Relationship between size of body and fecundity of female adult tussock moth.

of ponderosa pine (Figure 9) while, at the same time, they seemed to be relatively scarce on white fir. During heavy out-breaks defoliation of pine in the late instars is common, espe-cially when much of the fir foliage has already been depleted. However, migration of young larvae to pine foliage when fir foliage is still abundant has not been reported. This obser-vation infers that, in the absence of new fir needles, new pine growth might be selected before old fir needles. As a means of testing this hypothesis and making other comparisons of host selection, three trays, each with 25 fourth instar larvae and selected branches of foliage, were established in the field laboratory as follows:

Tray A. One branch of current year's pine needles and one branch of frost-damaged fir.

Tray B. One branch of second year pine needles and one branch of frost-damaged fir.

Tray C. One branch of current year's pine needles and one branch of normal fir foliage.

Branches were secured in water vials to prevent drying. Larvae had equal opportunity to feed on either type of foliage or change from one branch to the other. Amount of feeding on types of foliage was compared by collecting and measuring the frass under each branch in the trays.

Results after 12 days of feeding are illustrated in Figure 10. During this period many of the test larvae in the trays died

Figure 9. Douglas-fir tussock moth larvae in the sixth instar feeding on current needles of ponderosa pine. (Lab photo)

A.

B.

C.

Cumulative frass production (cc)

Old fir

New pine

Old fir
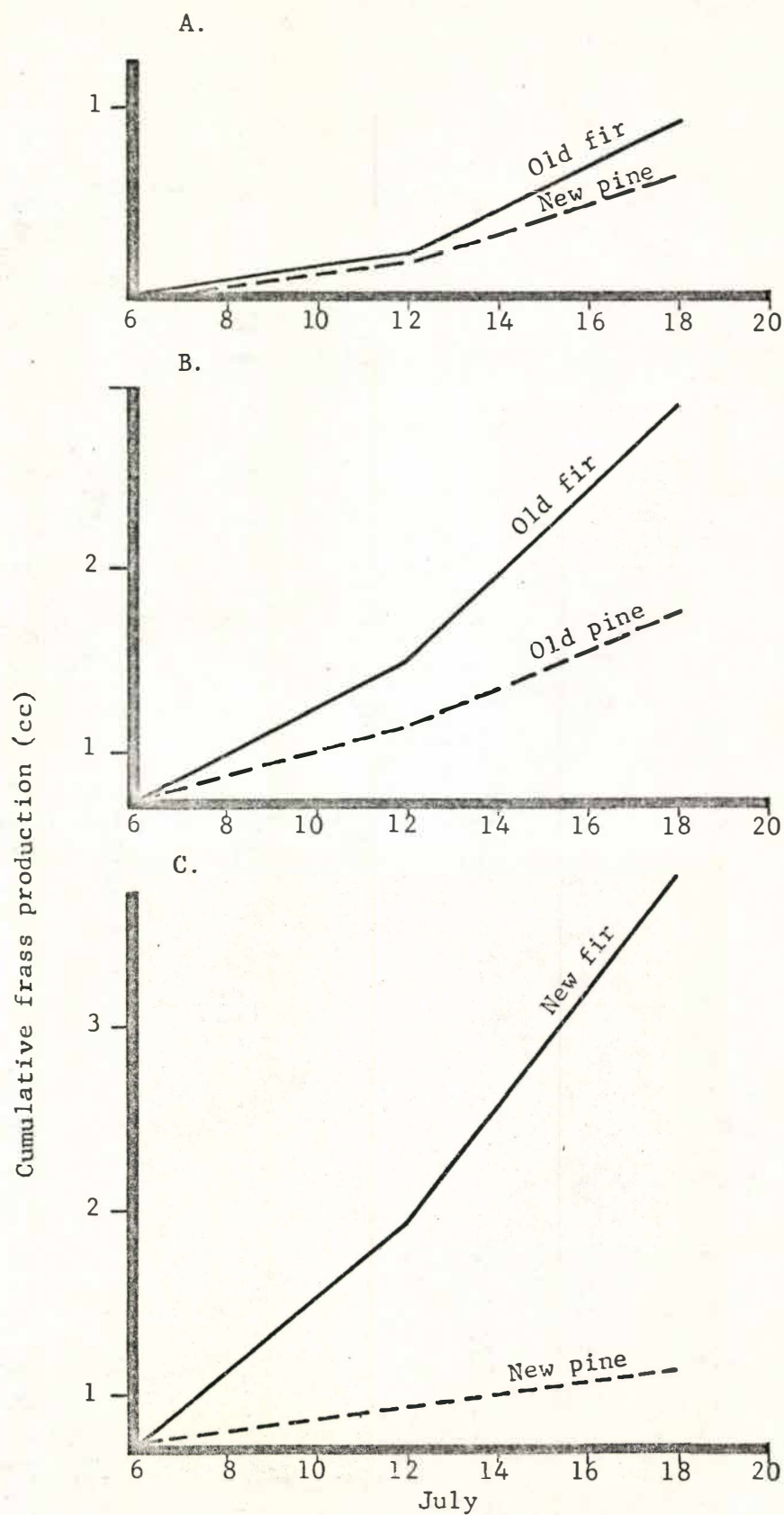
Old pine

New fir

New pine

July

Figure 10. Frass production by fourth instar larvae in three rearing trays in the laboratory when offered different types of foliage simultaneously.

from disease so that between-tray comparisons are not valid.
However, comparison between foliage types in the same tray
are indicative since each branch was available at all times
to the same number of larvae. In all of the tests larvae
fed at least as much and usually a great deal more on white
fir than on pine. Of most interest is that there was little
difference in frass production under old fir and new pine in
the same tray (Figure 10, Part A).

This tends to substantiate field observations that larvae fed
considerably on new pine foliage when only old needles were
available on fir. New growth flushed much later on pine than
on fir so that there was probably little migration of first-
and second-instar larvae to pine growth. Moreover, current
pine foliage may not be as suitable for these instars as for
older larvae. New fir foliage was vastly superior to new
pine foliage for feeding (Figure 10, Part C) which suggests
that optimum conditions for growth and development only occur
when this type of foliage is available. Frost, by removing
the favored food, obviously exerted a nutritional stress on
the population.

Effect of Light and Temperature on Larval Movement

Behavior of larvae is influenced by a number of external stimuli, espe-
cially temperature and light. Knowledge of how these affect larval
movement and eventual location of larvae in the tree can be particularly
important in designing a sampling program. General observations during
the summer, supported by several empirical type tests, provided some
information on larval behavior in the presence of different stimuli,
particularly light intensity.

In one test a 20-inch white fir branch with two prominent forks was
attached horizontally to the side of a large pine tree. The branch
was in direct sunlight with a measured intensity of about 9000 foot
candles and an air temperature of 96 ° F. A section of cardboard was
then used to shade one fork and one-half of the main stem leading from
the tree to the forks. Therefore, approximately half of the branch
was shaded and half in full sunlight. Shading reduced the light in-
tensity to 650 - 1900 foot candles and the air temperature to 85° F.
Ten late-instar larvae were then placed one at a time on the base of
the stem and observed as they crawled out the branch. Nine of the
ten larvae selected the shaded side of the branch. The procedure was
repeated except by moving the cardboard so that it shaded the other
fork, thus reversing the shaded and sunny sides. In the second trial
9 of 11 larvae again crawled out onto the shaded portion of the branch.

In another test 10 larvae were placed on a branch, all of which was in full sunlight. Observations were then made on their behavior and the position they selected on the branch. After 10 minutes all larvae had crawled to the underside of the twigs and needles and remained in that position for four hours. Then the branch was turned completely over to expose the underside to direct sunlight and higher temperatures. Again, within 10 minutes 9 of the 10 larvae had moved around to the underside. This behavior suggests that position on the branch is a result of response to light and temperature and not orientation to just the ventral side of the needle.

A third but less conclusive test involved a portable muslin cage which was placed around a six foot tree (Figure 11). The muslin shield reduced maximum light intensities by 80 to 90 percent and temperature about 6° F; humidity, however, increased for lack of ventilation. Cardboard sheets laid on top and against the sides of the cage reduced light even further. However, when larvae were placed on the tree little change in activity was noted from normal behavior in full sunlight conditions.

Figure 11. Portable muslin cage placed around a small white fir to modify environment while studying larval behavior.

General conclusions from these tests and other observations are that during daylight hours larvae move to avoid high temperature and/or light intensities. Apparently, the underside of needles and branches is at least temporarily adequate protection from these extremes. Whether or not larvae migrate in significant numbers to shaded trees or shady sides of trees, which is a characteristic that could affect sampling procedures, is not yet known.

Larval Activity Rhythms

Activity of larvae varies through the day and night and with the age and instar of the insect. Edwards (1965) studied this behavior in the laboratory and found that young larvae exhibited mainly diurnal activity, with nocturnal activity apparently inhibited by low temperatures. Late instar larvae, on the other hand, were chiefly nocturnal. At Corral Creek no observations were made on rhythmic behavior of early instars, but several studies were carried out under natural conditions on activity patterns of late instars.

In one experiment counts were made of 100 larvae at different times of the day to record the number that were moving about or feeding. The first counts were made on fourth, fifth, and sixth instar larvae over a 12-day period and the second counts on sixth instar larvae in one day. Percent of observed larvae that were feeding or active and the temperature at the time of the observation are plotted for different times of the day in Figure 12. Very little activity occurred at mid-day in either of the studies, but young larvae (Part A) may have been more active late in the morning than were older larvae (Part B) as also suggested by Edwards. Feeding seemed to make up a large proportion of total activity which indicates that wandering and feeding are closely associated and probably occur at the same time of the day. Reduced activity also coincided with rising temperatures that remained high most of the afternoon; it is, therefore, difficult to separate a light rhythm from what might be a negative response to temperature.

A similar test was repeated using a sample of nine and another a sample of ten larvae, each of which was placed individually on different branches. Observations were then made through the day on the same individuals. The general pattern of results as shown in Figure 13 are again similar to those already reported. Total activity was least at mid-day when temperatures were highest and seemed to be substantially greater in the morning, late afternoon, and evening.

Rate of larval movement at different times of the day was examined by measuring the distance between position of each of ten larvae from one hour to the next and assuming that this was the shortest distance traveled during that hour. Results from these calculations contradict the previous experiments somewhat since some movement was recorded at mid-day when temperatures were highest (Figure 14). Discrepancies, however, can be expected when such a small sample is used. Over a 15-hour
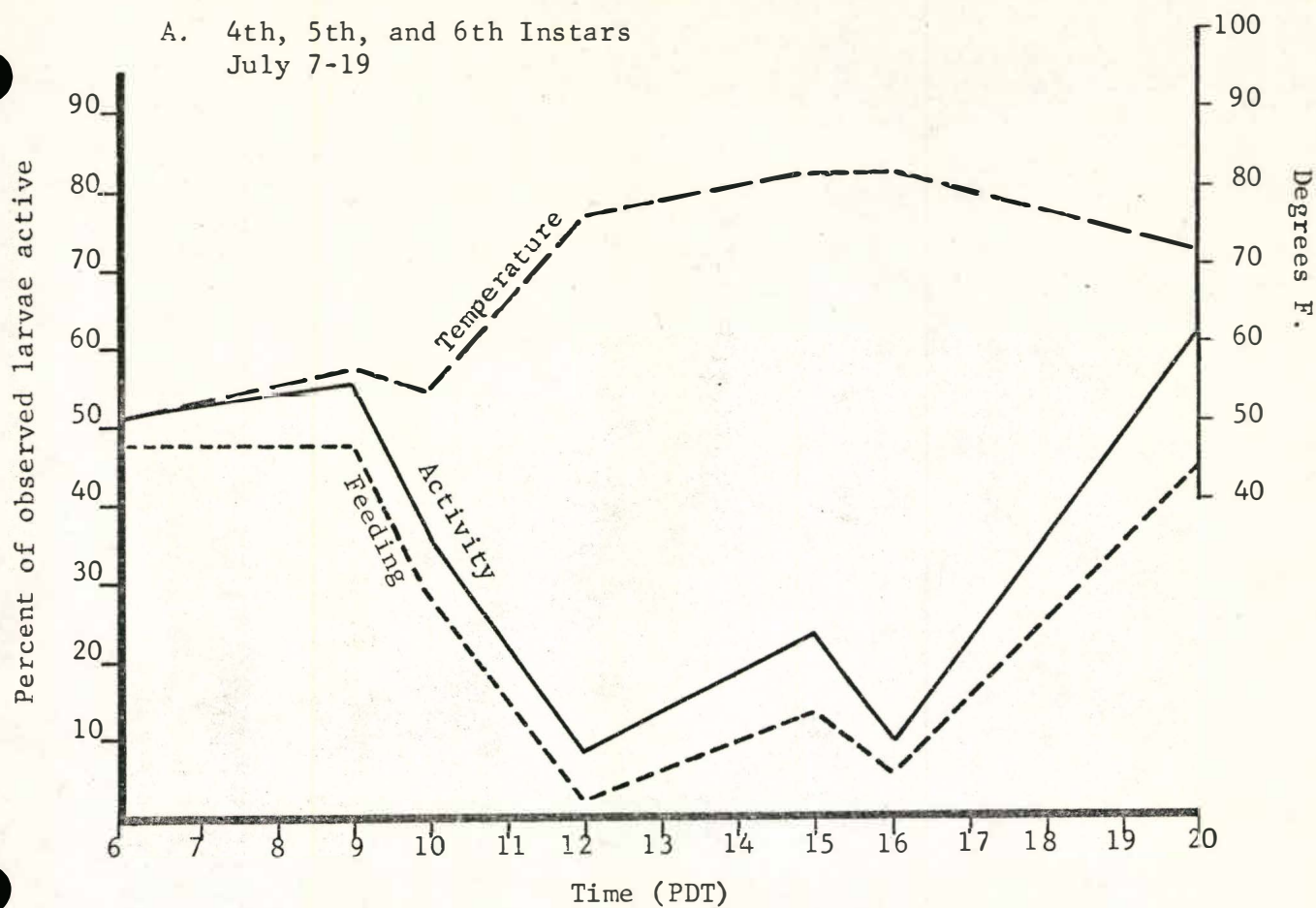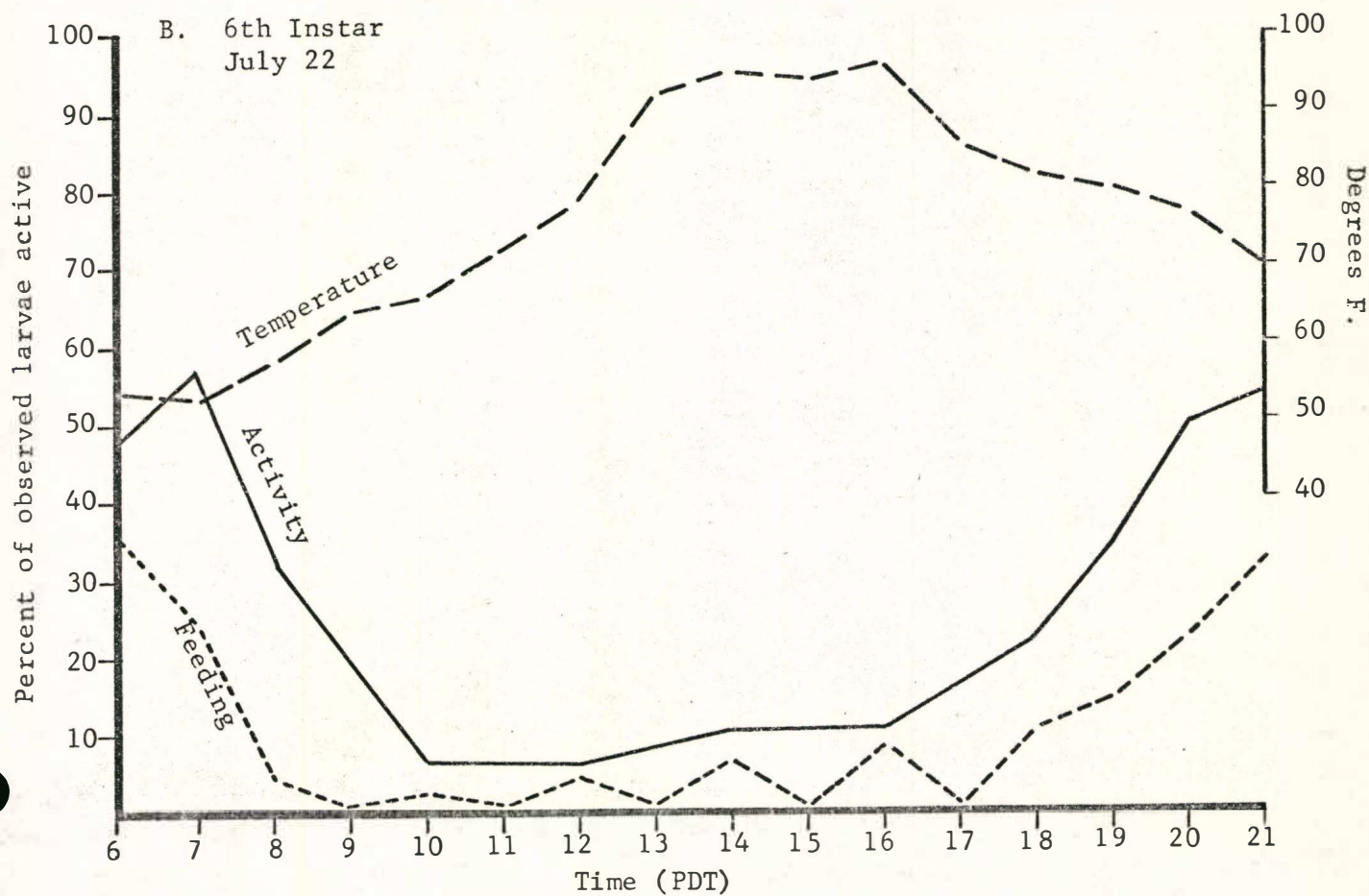
Figure 12.   Activity of tussock moth larvae in the field at different
             times of day.
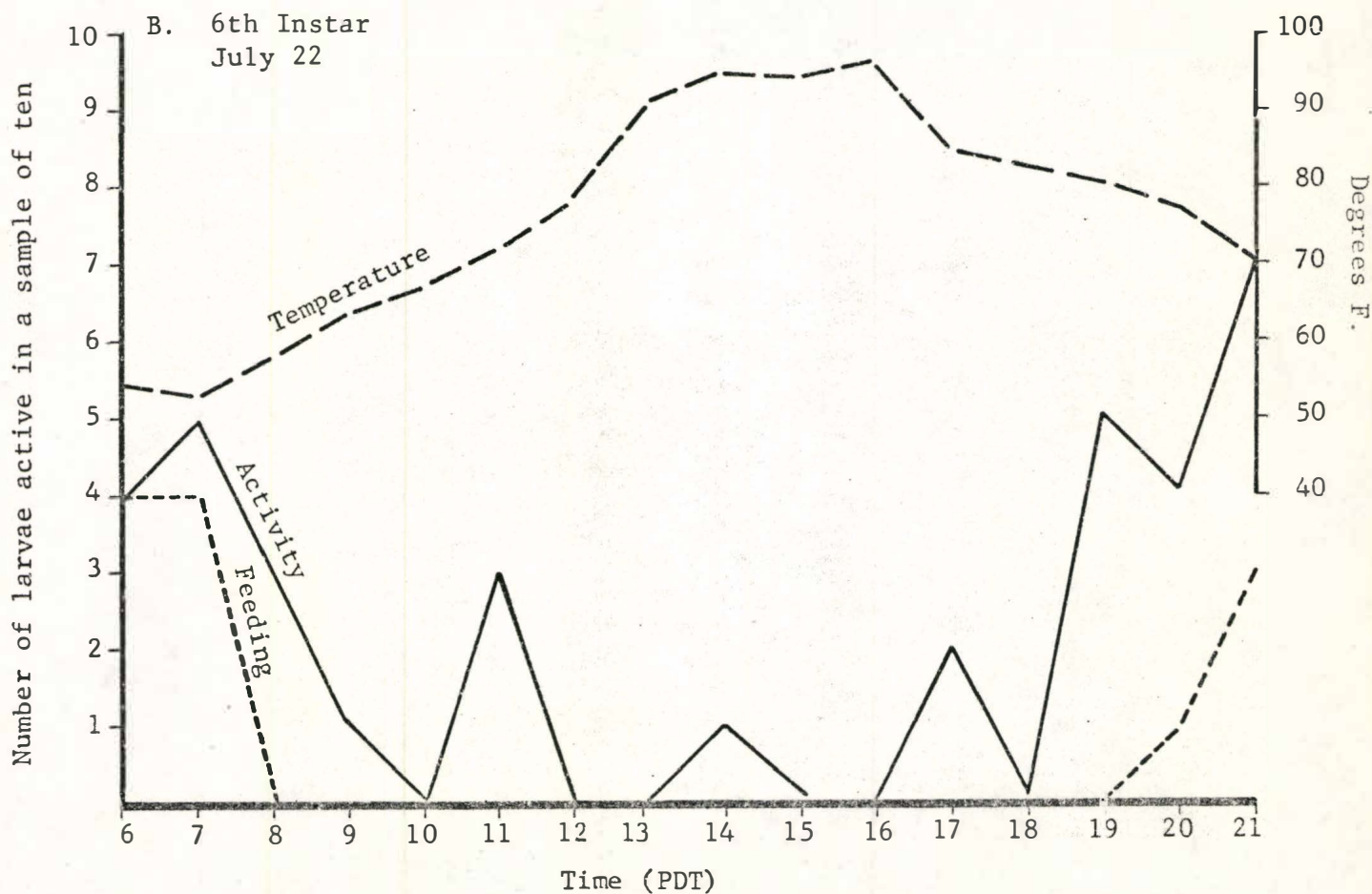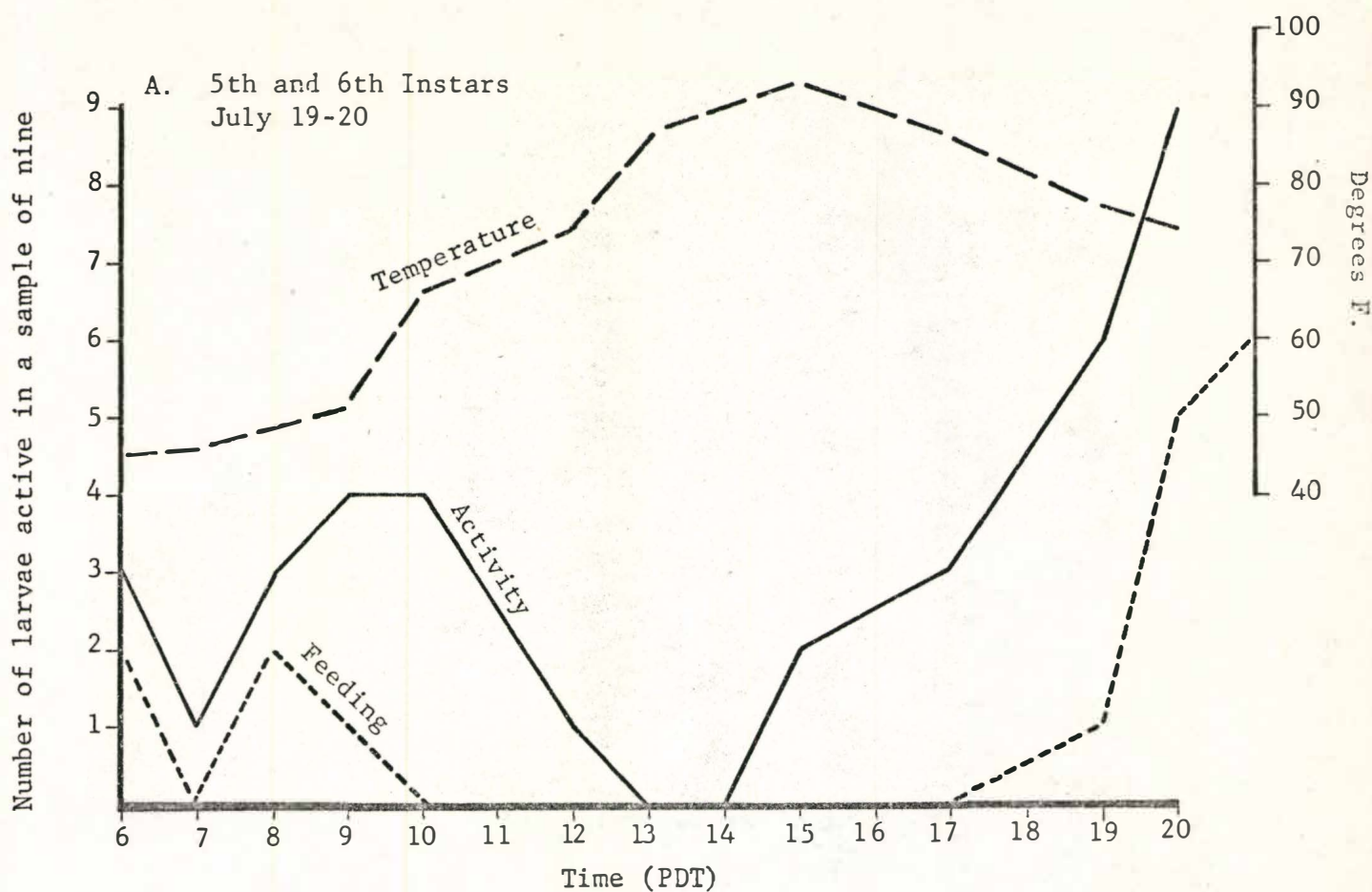
Figure 13. Activity of larvae in a specific sample in the field at
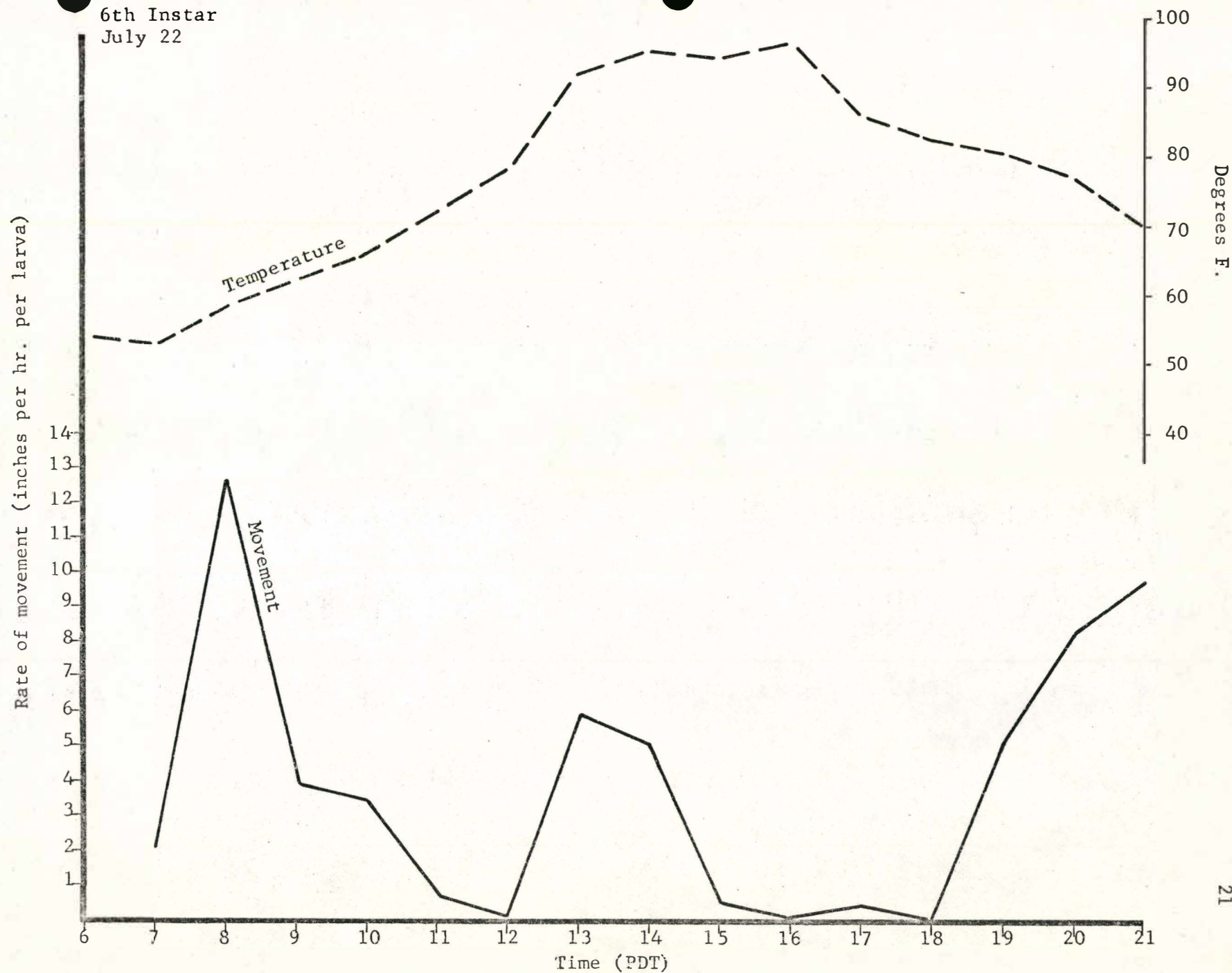   different times of day.

Figure 14. Distance of movement by larvae on branches at different times of the day. (Based on the shortest distances traveled by 10 larvae).

period the average larva traveled a minimum distance of 40 inches or about 2.7 inches per hour. During periods of high activity, as in the morning or evening, the average distance traveled per hour was much greater.

In a final study of activity rhythms, feeding behavior, of sixth instar larvae was investigated for a 48-hour consecutive period. Two branches of white fir were attached to the trunk of a large pine with muslin baskets beneath to catch the frass from feeding larvae (Figure 15). Twenty-two larvae were placed on each branch and the combined frass collection from both baskets was measured every four hours. Results are plotted in Figure 16 with the respective temperature at the end of each four-hour interval. Maximum frass production for both 24-hour periods occurred at night with the peak being reached around midnight. The relationship between frass production and temperature in Figure 16 is remarkable for its inverse symmetry; however, this is not to imply that feeding is strictly controlled by temperature, since high temperatures are also associated with high light intensities. It is particularly interesting that night temperatures in the low 50's do not seem to be a detriment to feeding by late instar larvae. Edwards found that early instar larvae, which were normally active during the day, were active at night only when the temperature was at least 20° C. (69° F). Our studies indicate that late instar larvae are relatively inactive during the day, especially during times of extreme temperature and light. It is not known to what extent local weather might alter the diel cycle.

Figure 15. Muslin baskets beneath two white fir branches attached to pine bole for catching frass from feeding larvae.
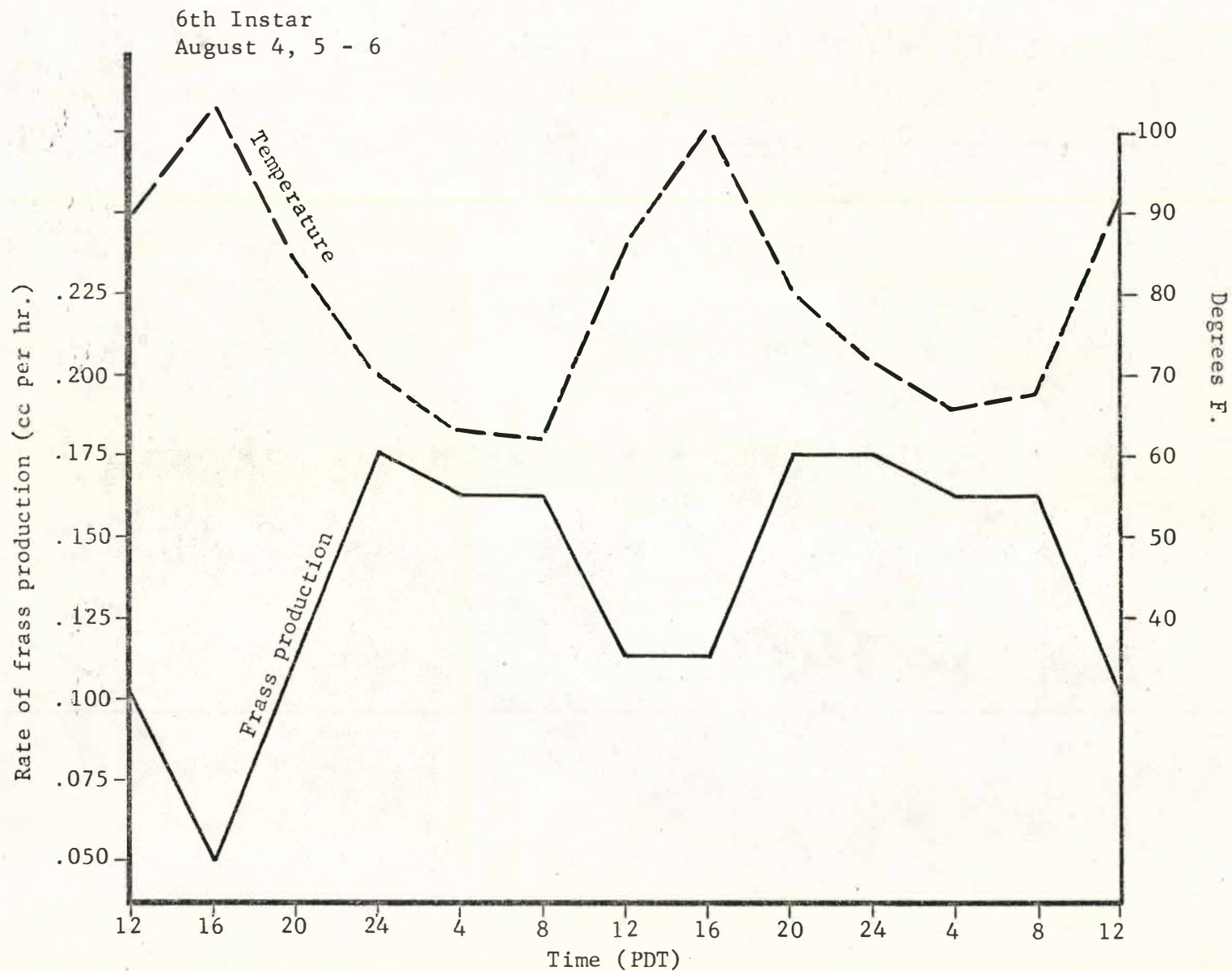
Figure 16. Frass production in the field by 44 larvae at different times of the day.

Distribution of Larvae on Tree Branch

As already discussed in the section on late frost and food quality,
early instar larvae feed extensively on new needles, but as these
are depleted and larvae develop they feed progressively more on old-
growth foliage. This pattern of feeding determines the distribution
of larvae on the tree as demonstrated by a series of successive counts
of larval position.

Ten white fir trees between 10 and 18 feet tall, which had substantial
amounts of new needle growth not injured by the frost, were selected
for examination. To determine relative larval position, two separate
parts of the branch were mapped: (1) the branch tip, that included
all new growth plus three inches of the woody twig with only old
foliage; and (2) the remainder or "inner" branch. Larval counts
lasting five minutes on each tree were made during which the number
of larvae on both positions of the branch were recorded. In four
weekly measurements 733 larvae were counted and classified according
to location on the branch.

As expected, young larvae were highly concentrated on tips early in
the summer, but as the season progressed they moved further back on
the branch (Figure 17). On trees with much of their new growth
destroyed by frost, larvae were especially clustered on new growth
that had escaped damage. Counts as high as 25 second- and third-instar
larvae on one undamaged tip were not uncommon. Even though larvae fed
progressively further back on the branch they remained mostly in the
outer 15 to 18 inches of main or side branches which constituted most
of the foliated portion of the tree. Only last instar larvae were
occasionally found on the tree bole. These results suggest that foliage
areas alone are an adequate universe on the tree for sampling larval
populations of the tussock moth.

DISCUSSION AND RECOMMENDATIONS

In population sampling studies carried on concurrently with the biology
and behavior studies described here, survival of early instar larvae
was found to account for the largest portion of variation in ultimate
larval survival. Furthermore, the greatest decline in larval numbers
also occurred at that stage, although a high mortality rate is not
necessarily responsible for a large amount of variance. This means,
at least in the Corral Creek outbreak, that mortality of young larvae
was especially prominent in establishing the course of decline in 1966.
Results of behavior studies described in this report now strongly
suggest that, in addition to virus disease, poor food quality which
caused starvation and dispersal was also a major factor affecting
survival of young larvae. These findings imply that rate of mortality
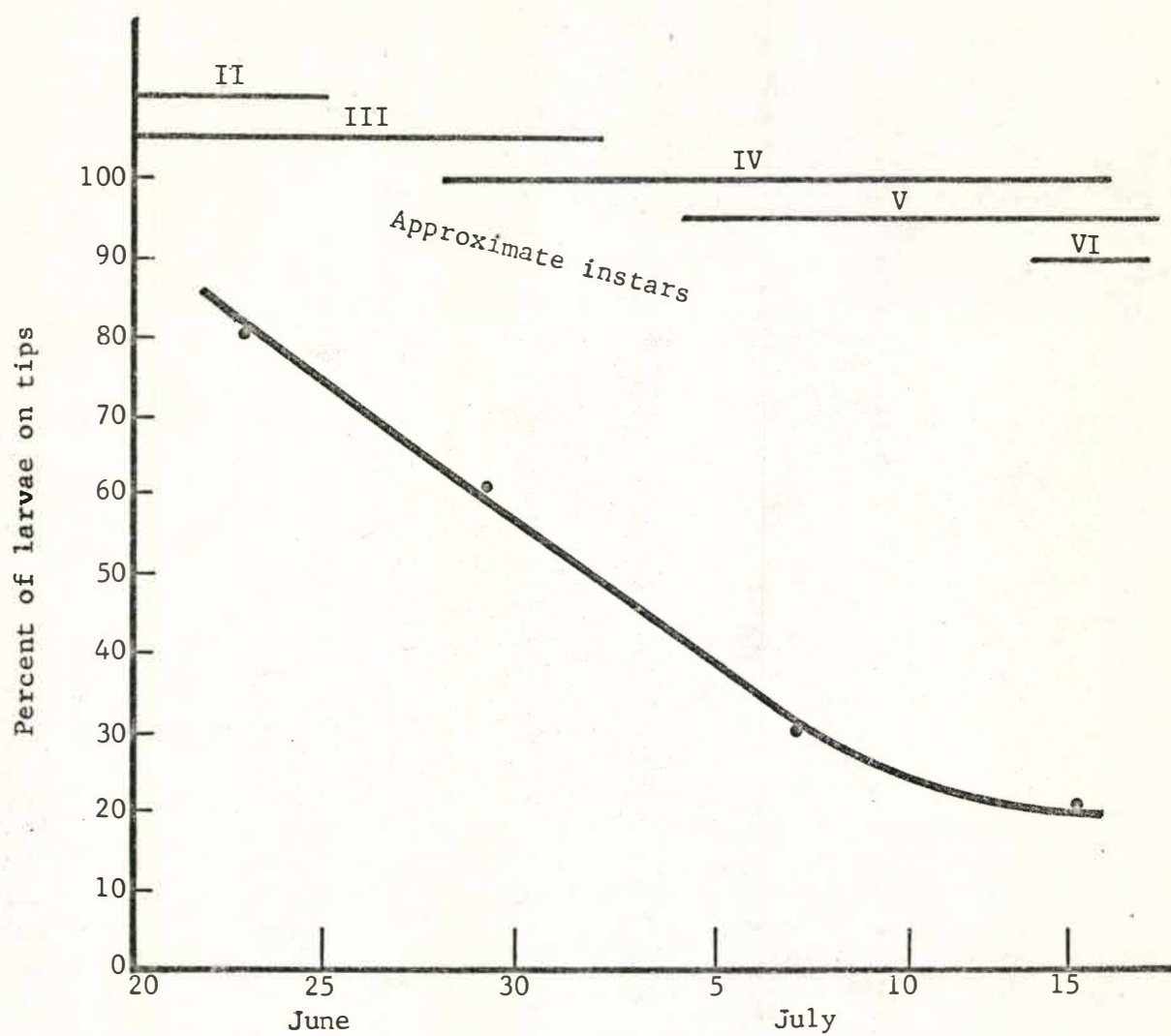
Figure 17.   Position of different aged larvae on white fir branches.

at this stage could be a determining factor that frequently sets the course of population trends. The late frost in 1966 was largely responsible for the scarcity of acceptable food at Corral Creek; however, under different conditions other factors such as parasitism, predation, stand structure, crowding and others could have a similar impact on early instars and, thus, be equally capable of influencing the trend of tussock moth populations. It is logical that future research should be directed toward isolating those key factors which have the potential of regulating populations so that efforts can be made toward favoring their action.

Most of the studies described in this report were small and inconclusive, but they do provide considerable data on some phases of tussock moth biology where information was seriously lacking. As mentioned, the studies of food quality especially have revealed a number of behavioral and nutritional features which may have a strong impact on population trends of the tussock moth in different localities. The results of studies on larval distribution, activity rhythms and response to light and temperature will be an aid to further development of sampling techniques and possibly the perfection of virus spray methods. Although much remains to be learned about the tussock moth, research efforts should first be concentrated on those subjects which seem to be associated with causes of outbreaks or which appear to be promising avenues toward the eventual regulation of tussock moth numbers in forest stands. With these objectives in mind the following general subjects of study are recommended for priority attention in future research on tussock moth biology:

1. Test for the presence of a sex attractant in virgin female moths and its effectiveness in luring wild male moths to field traps.

2. Identify the important parasite-predator complex and investigate its impact on the population.

3. Investigate possible effect of variations in microclimate, local weather, elevation and aspect on generation survival and environmental resistance factors.

4. Study effects of larval crowding on survival, rate of development, body size and fecundity.

5. Expand studies of food quality to include effect of foliage from different trees and sites on survival, development rate, size, fecundity and egg viability.

6. Study short and long range dispersal of early instar larvae.

7. Look for significant quality differences between individual larvae that may be genetically controlled.

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